Population growth from birth and death

Jesse Brunner

2022-10-06

We have been talking a lot about population growth and rates of replication, but I am guessing it has seemed a little…abstract to many. After all, we keep making these silly assumptions like *everyone doubles themselves each time step* or *everything is happening all the time all at once*. But of course our biological intuition does not match these assumptions. Most animals, for instance, are born (or hatch), grow, eventually become reproductive, and then reproduce over one or more bouts. They may also be more or less likely to die during different periods of their lives. *None* of that seems constant or to translate simply to λ or r.

Using averages to get around the biology

First, we should note that when we are discussion the population multiplier (λ) or intrinsic growth rate (r), we are really thinking of the average across the entire population, including those in different stages or ages[1]. So, for instance, for humans we might simply figure out how much the population grows from one year to the next and then back-calculate what r must be from $N(\text{Year 2}) = N(\text{Year 1}) \times e^{r \times 1\,\text{year}}$), which is a way to average the *per capita* growth rate over all of the people, young and old.

But still. There's all this important biology about how long animals live, when they become reproductive, how many offspring they have, and how all of this changes over time. Surely there is some way to work out λ or r from *that* sort of information?

You, my friend, are in luck!

From life tables to R_0

It is probably easiest to work with a simple example. Let me consider an idealized mouse (*Peromyscus* spp.) in nature[2]. First, let's consider their probability of surviving over time. A mouse might rarely live to see 2 years of age in nature (and up to 8 years in captivity—Nature is red in tooth and claw, and all that, huh?), but probably a more realistic range is 95% chance of surviving to 12 months. Their probability of survival might look like this:

x	l_x
0	1.00
1	0.78
2	0.61
3	0.47
4	0.37

[1] And depending on the study, sexes. Often we just count females and ignore males when thinking about demographics. Males are not exactly rate limiting, after all; they just provide sperm.

[2] I tried to find information for the guinea pig, but relevant information was not easily accessible.

x	l_x
5	0.29
6	0.22
7	0.17
8	0.14
9	0.11
10	0.08
11	0.06
12	0.05

Here x is the time step, in months[3], from birth ($x = 0$) through one year ($x = 12$ months). l_x is the probability of surviving to that time[4]

For fun we can plot this probability of surviving over time (months) on linear and logarithmic scales.

Notice that on a logarithmic scale, the decline in survival is constant. This is a hint that the probability of surviving from month to month is essentially the same—a constant rate—whether young or old. Indeed, I assumed a 75% chance of survival per month. (And this is a reminder that constant decline is very similar to constant increase *a la* exponential growth models.)

Second, we can add into our table the average reproductive success from individuals of each stage or age. Importantly, this is averaged across all of the individuals, whether they reproduce or not, and have large or small clutches[5]. Importantly—and perhaps obviously—this only accounts for individuals alive to actually reproduce. So we can think of it as the average clutch size of (live) females of age x. We call this value age-specific "fecundity" and represent with the symbol m_x.

Mice can become reproductive within two months and then have a clutch of 1-3 (depending on size) every two months, so on average—accounting for the fact that some mice reproduce immediately at two months and others might wait until three months or four—we get something like this[6]:

x	l_x	m_x
0	1.00	0.00
1	0.78	0.00
2	0.61	0.00
3	0.47	0.50
4	0.37	0.75
5	0.29	1.00
6	0.22	1.25
7	0.17	1.50
8	0.14	1.50
9	0.11	1.50

[3] Or whatever time step we're interested… perhaps weeks for *Daphnia* or years for horses.

[4] Why l_x? Convention. I'm going to stick with conventions throughout so that if you ever want to look this stuff up you can.
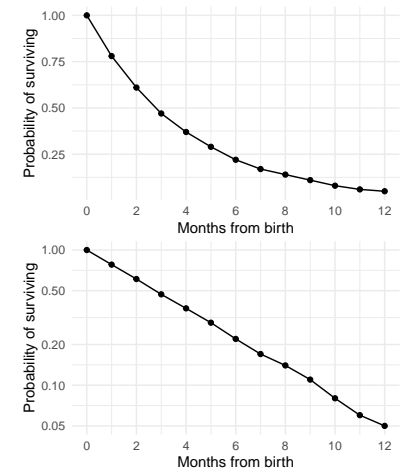

Figure 1: Average survivorship of imaginary mice over 12 months.

[5] Also, let's assume we are only tracking female survival and reproduction; the males can be safely ignored.

[6] With nice fairly round numbers to keep things simple

x	l_x	m_x
10	0.08	1.50
11	0.06	1.50
12	0.05	1.50

Now here's the question: would a population of mice with these patterns of survivorship (l_x) and fecundity (m_x) grow? Shrink? Just replace itself?

Initially this is a hard thing to answer. Sure, females that are 5 or more months old produce a lot of babies, but then again, relatively few actually survive that long. Moreover, how do we merge these gains and losses in a coherent way to estimate the population growth rate?

A first step is to rephrase our question in a more tractable form: *What is the expected reproductive output of the average (female) mouse over her entire expected lifetime?* We can call this value R_0. If a female just replaces herself, on average ($R_0 = 1$), then the population must be just replacing itself, yes? And if a female produces two offspring, on average ($R_0 = 2$), then the population must double in each generation, meaning it is growing (fast!). If instead an average female only generated 3/4 of an offspring, on average ($R_0 = 0.75$), over her entire lifespan then she not even replacing herself and the population would shrink (by 25% a generation). Let's see how this works.

The key is that the expected reproductive output of females of a given age (e.g., $x = 5$ months old) is they must have survived to that point—given by l_5—and then have their clutches of average size m_x. We can thus figure out the expected reproduction of each stage as the product, $l_x \times m_x$. Let's add this into our table:

x	l_x	m_x	$l_x m_x$
0	1.00	0.00	0.000
1	0.78	0.00	0.000
2	0.61	0.00	0.000
3	0.47	0.50	0.235
4	0.37	0.75	0.277
5	0.29	1.00	0.290
6	0.22	1.25	0.275
7	0.17	1.50	0.255
8	0.14	1.50	0.210
9	0.11	1.50	0.165
10	0.08	1.50	0.120
11	0.06	1.50	0.090
12	0.05	1.50	0.075

We can see that we expect no reproductive output from 1-month-olds or two-month-olds—they are pretty likely to survive to these stages, but their fecundity is zero. We then expect a bit less than half of the mice to survive to 3-months, and

each of those would have, on average, half an offspring, which means we expect the average mouse to have a reproductive output of a bit less than quarter in their third year. We can also see that the gains in fecundity—bigger clutches—of older mice are offset by their lower survivorship—probability of surviving to that point—which means we get about the same expected reproductive output from 3–7 month-olds!

Now, finally, to get the expected reproductive output of the average mouse over its entire expected lifespan—from mice age zero to mice age 12 months—we can simply add up these $l_x m_x$'s. That's it! Or mathematically[7] [8],

$$R_0 = \sum_{x=0}^{x=L} l_x \times m_x.$$

So, should we expect our hypothetical mouse population to shrink, stay the same, or grow? You now have all of the information. What do you think?

Figure 2: Monthly and cumulative expected reproductive output from our example.

From life tables to lambda!

So I promised we would get to our more traditional metrics of population growth: λ and r. For that we just have one or one-and-a-half steps.

Recall that R_0 is the expected reproductive output of an average female over her expected lifespan, but it can also work as a multiplier. If $R_0 = 2$ then a population of 100 mice would become 200 in the next generation, yes? This is very much like λ, only its time span is a generation rather than a time step (e.g., year or month). Mathematically we can write:

$$R_0 = \lambda^T,$$

where T is the average generation time[9].

Our task, then, is simply to figure out the generation time. I'm going to skip most of the justification and go straight to the formula, but just know that this is essentially a way of finding the average time from birth to reproduction.

$$T = \frac{\sum x \times l_x m_x}{\sum l_x m_x} = \frac{\sum x \times l_x m_x}{R_0}$$

In our case, this amounts to $T = 6.5$ months.

So we know that $R_0 = 1.992 = \lambda^{6.5}$, which we can re-arrange[10] to $\lambda = 1.922^{\frac{1}{6.5}}$ \$ = 1.112.

To get to the value of r, the intrinsic growth rate, we simply need to remember that $\lambda = e^r$, so $1.112 = e^r$. If we take the log of both sides we get $r = \ln(1.112) = 0.106$.

All of these values—R_0, λ, and r—say the same thing: this population should grow. They have different uses, so ti is nice that they are (pretty) easy to convert between.

What's the use?

It turns out that this life-table approach to estimating population growth[11] are really useful when thinking about all sorts organisms, from species of conservation concern, invasive species, invertebrate vectors, and pathogens. It is even possible to use a similar approach for *infections* spreading in a population. You may have heard estimates of "r naught" for COVID, well that is the British pronunciation of R_0. It is, in effect, the same thing: the expected number of secondary cases caused by an infected individual over the duration of its infection in a wholly susceptible population[12].

We can thus take basic biological information, or reasonable guesses, and make estimates of whether a population of a species of interest will grow or shrink. We can also play with the values to see what whether, say, increasing or reducing fecundity at a certain stage might increase or decrease the overall population growth rate very much. It gives us a way to translate things we might try to do, like increasing larval tick mortality through the use of an acaricide or decrease mortality of young sea turtles by modifying shrimp trawling nets, to likely population-level outcomes. In short, this sort of thinking is incredibly useful and, I suspect, now that you know what it is, you will probably see it all over the place.

[11] And related methods that rely on life-history matrix models

[12] This last bit is so we can avoid the inherent density-dependence that arises when infected individuals die or recover and become immune.